

HETEROSTYLY AND HOMOSTYLY IN  
LITHOSPERMUM CANESCENS (BORAGINACEAE)

H. G. BAKER

In the Boraginaceae, heterostyly of the distylous type was first investigated experimentally by Hildebrand (1864, 1865) and Darwin (1877) who both worked with species of *Pulmonaria*. Its occurrence in the family, however, had been noticed earlier by Torrey (1856), especially in *Amsinckia*, and Gray (1859) records it for *Lithospermum*. Much more recently, Johnston (1952), in his taxonomic survey of *Lithospermum*, took care to distinguish heterostylous from homostylous species and used the distinction in his key for their identification. However, no experimental work has been done on this genus so that our knowledge of the population biology of its species is still at a primitive level. Therefore, it is of interest that two works published by nineteenth century botanists dealing with heterostyly in *Lithospermum canescens* (Michx.) Lehm., one of the showy North American species, appear to have remained unknown to twentieth century writers on the genus even though they contain items of considerable moment.

The first of these neglected works is by Erwin Smith (1879). This is of more than merely historical interest because it also records the existence of homostylous plants of *L. canescens* amongst the plants which he collected in Michigan. In Johnston's recent treatment, *L. canescens* was considered to be exclusively heterostylous and, indeed, no other species of the genus has been recorded as containing indisputably heterostylous and homostylous plants. This need not be surprising for Baker (1960) has given reasons for believing that speciation is likely to follow quickly after a change in breeding system (and heterostyly promotes allogamy while derived homostyly is generally associated with a greatly increased proportion of autogamous seed-production).

Translating Smith's remarks on proportions into percentages, it would seem that roughly 59% of the plants



which he saw were short-styled (with stamens inserted at the mouth of the corolla-tube) while only 39% were long-styled. In the long-styled plants the length of the style varied from being included within the corolla-tube to being conspicuously exerted, an appearance which could result from the sampling of flowers of different ages should there be a differential elongation of corolla-tube and style during maturation of the flower. The remaining 2% of plants would be classified nowadays as "short-homostyles". Even these showed some variability, the anthers standing either at the level of the stigmas or just above them. Particularly striking, however, was a tiny proportion of homostylous plants in which the stamens are inserted at two levels, two of them above the stigma and three on a level with it.

The accuracy of such an observation is testified to by the subsequent description of an unequal (or zonal) insertion of stamens by Johnston (1952) in *Lithospermum tournefortii* Johnston (heterostylous) and *L. decumbens* Vent. (probably homostylous), as well as in several other genera of the Boraginaceae. However, it is in the published accounts of the floral structure of *Amsinckia lunaris* Macbr. (Macbride, 1917; Suksdorf, 1931; Ray and Chisaki, 1957) that the closest parallel may be seen. Here, probably as in *Lithospermum canescens*, a heterostylous species has produced a homostylous variant in which the stamens are inserted at two levels, one of them corresponding with the height of the stigma and almost certainly leading to a high proportion of self-pollination. In *Amsinckia lunaris*, according to Ray and Chisaki, the pollen grains from the two lower anthers are smaller than those from the upper trio (which may function in cross-pollination). It would be most interesting to know if a similar situation obtains in the unusual plants of *Lithospermum canescens*.

In view of this report of homostylous plants of *L. canescens* from Michigan, a survey was made of the floral structure of specimens from a variety of States in the herbaria at the University of California, Berkeley, and at



Stanford University. Also Dr. Paul Grun and Dr. R. B. Channell kindly made observations on material at Pennsylvania State and Vanderbilt Universities, respectively. Unfortunately, no homostylous specimens were found. Overall, however, 39 short-styled plants were observed along with 24 long-styled. This preponderance of short-styled plants tallies with Smith's (1879) observation from Michigan. If field-studies should show this to be a regular feature of naturally occurring material, it might be interpreted most reasonably as indicating that some self-pollination occurs (otherwise the two forms might be expected to occur in roughly equal numbers). A preponderance of short-styled plants could be produced if this type is self-pollinated considerably more frequently than is the case with the long-styled form, through pollen falling down the corolla-tube. Another possible cause of such a disparity in numbers, although of lesser likelihood, would be that both forms are selfed with roughly equal frequency but that the allele producing the long-styled condition is the genetical dominant. On selfing the heterozygous form produces both kinds in its progeny while the homozygous recessive form produces all recessives, creating an excess of this form. However, in almost all cases where the genetics of a distylous system is known it is the short-styled form which is genetically dominant (cf. Lewis, 1954). Only in the Plumbaginaceae is there good reason to believe that the opposite is true (Baker, 1954 and unpub.), and preliminary results for the Boraginaceae from the genus *Amsinckia* (Ray and Chisaki, 1957), as well as a modern interpretation of Darwin's (1877) results with *Pulmonaria*, both suggest a contrary situation; that the short-styled condition is dominant.

Another, apparently unique, feature of heterostyly in *Lithospermum* is a difference in *shape* between the pollen of long-styled and short styled plants. To Johnston (1952), his discovery of this shape-difference correlated with heterostyly demonstrated "a type of pollen dimorphism previously unreported." However, in 1880, in the second of these neglected papers, C. E. Bessey described heterostyly in material of *L. canescens* from central Iowa and included not only



statistics on the sizes of the pollen grains of the two kinds of plants but also these comments on their shapes, "pollen grains ovoidal, slightly constricted in the middle" (on short-styled plants) and "pollen grains oblong, much constricted in the middle" (on the long-styled plants). The descriptions accord quite well with Johnston's more detailed observations made three-quarters of a century later.

This overlooked, earlier description of pollen shape differences associated with heterostyly recalls that dimorphism in sculpturing of the grains was described as a part of flower dimorphism in the Plumbaginaceae by Macleod in 1887, but that this lay unused until Kulczyński (1932) applied it to the identification of fossil pollen. Actually, neither Bessey's nor Macleod's description of pollen dimorphism was the first report of such a phenomenon, for it had been seen in the Rubiaceae as early as 1868 by F. Müller (1869), the significance of this demonstration remaining unnoticed until recently (Baker, 1956).

In fact, Bessey's short paper was more concerned with a description of the variable relationship between stamen and style lengths in another species, *Lithospermum longiflorum* Pursh (which is now considered synonymous with *L. incisum* Lehm.). In this species, Bessey considered that heterostyly might be in process of development. However, in view of its production of cleistogamic flowers on a regular seasonal basis, it seems more likely that his alternative suggestion, that this is a species which has moved toward inbreeding rather than away from it, is the correct one.

However, had Bessey made his observations just a few years sooner, it is unlikely that they would have been relegated to the obscurity which has been their fate. On May 22, 1877, Asa Gray wrote to Charles Darwin saying, "I asked my good correspondent Prof. Bessey to see if *Lithospermum longiflorum* (= *angustifolium*) being cleistogamous later, is, like its relatives, also dimorphous. Here is his first reply just in season to send you by this post. I forgot to ask him to examine *pollen*. I will do so" (unpub. let-



ter in Gray Herbarium, quoted from microfilm copies kindly lent by Dr. Hunter Dupree).

Darwin replied on June 4, 1877, in a letter which, because it does not mention the genus involved, has always been a mystery (cf. transcript in Holbrook, 1939). Now, we can see that it was to *Lithospermum incisum* that Darwin was referring when he wrote, "Prof. Bessey's case has come too late, as the sheets on this subject are printed ..... The pollen grains and stigmas ought to be compared. The case seems to be well worth careful investigation and I would have given my eyes for seeds formerly; but now I have done with the subject." He went on to give instructions for Bessey on methods of observation and experimentation and point out that, "the case may be one merely of great variability or it may be one of incipient heterostylism." Bessey appears to have given some heed to the instructions because his paper did not appear till three years later. Meanwhile, Darwin (1877) had published the famous book to which he was making reference in his letter — "The Different Forms of Flowers on Plants of the Same Species."

Surprisingly, Asa Gray, himself, never made a clear statement on dimorphism in *L. canescens*. In the "Synoptical Flora of North America" (Gray, 1878, and subsequent editions) his sole comment reads, ". . . in one form style about the length of the tube and stamens, inserted below its middle." Even with the deletion of the comma, one is merely left to infer the existence and appearance of a second form.

Knuth (1899, page 120; in translation 1909, page 137) added to the camouflage of Bessey's discovery by giving an erroneous reference in the statement, "Darwin describes the flowers of this species [*L. canescens*] as either heterostylous or very variable in regard to the length of the style." Actually, Darwin never described the heterostylism of any species of *Lithospermum* and, in all probability, the statement should have referred to Bessey and to *L. incisum*! Similarly, Knuth credits Darwin with a de-



scription of cleistogamous flowers in *L. incisum* (Knuth, 1899, page 120, as *L. longiflorum* Pursh; in translation 1909, page 137, as *L. angustifolium* Michx.). Once again the credit should have been Bessey's. On another page, however, although rather inconspicuously, the same author does give Bessey credit for having seen heterostyly in *L. canescens* (Knuth, 1898, page 62; in translation 1906, page 50).

Thus, despite a history of confusion and neglect lasting for the larger part of a century, the reproductive biology of *Lithospermum canescens* is commended to the attention of field-botanists and experimentalists living within its geographical range in the eastern half of North America. This species promises to reward the student of natural populations through variations in the proportions of the various flower-forms and the genetical studies which these may make feasible. — BOTANY DEPARTMENT, UNIVERSITY OF CALIFORNIA, BERKELEY, CALIFORNIA.

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## A NEW SPECIES OF *PANICUM* FROM NEW JERSEY

JASON R. SWALLEN

A specimen of *Panicum* was received recently for identification from Bayard Long of the Academy of Natural Sciences of Philadelphia, which has proven to be new. It was collected by Frank Hirst, an active amateur botanist in southern New Jersey, who recognized it as an unusual plant, and in whose honor the species is named. "It occurs dominantly in a small woodland pond in the pine barrens — growing in the water, much as *Panicum spretum* often does. This is a most interesting pond, the *Panicum* being